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Flocking and Seasonal Movements of *Quelea quelea* and *Agelaius phoeniceus* in Relation to Crop Damage

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Introduction

Bird pest problems in agriculture have proved difficult to resolve due in large part to the behavioural versatility associated with flocking. Flocking can facilitate learning through the use of colonial information centres by allowing birds to sample a large area in a short time and to communicate the locations of preferred foods. The array of food choices available to birds can be complex. Sampling is a continuous activity by which flocks learn to distinguish crop types, varieties, stages of maturity and field locations. They seem to learn to avoid only those sites treated with a chemical repellent, or to accept the presence of a frightening device after initially avoiding it. Flocking also concentrates damage resulting in locally severe losses. This is often a more important aspect of the damage than is overall countrywide losses. In addition, flocks can quickly change the focus of damage. Flocking and crop damage are often associated with seasonal migration, the spatial and temporal patterning of which can vary from one locality to another.

The major bird problems, when measured by scale and intensity of losses, involve granivorous species that have evolved in grasslands that are

characterized by seasonally abundant, but patchily distributed seed production whose maturation is staggered along a latitudinal or seasonal gradient (see Wiens, 1976, for a discussion of patchy environments). Opportunistic feeding, rapid learning of the location and timing of seed availability, flocking and migration are adaptations to such a transient and shifting food supply (Wiens and Johnston, 1977). Two outstanding examples of pest species that exhibit these characteristics are the red-billed quelea (*Quelea quelea*) of grassland Africa and the red-winged blackbird (*Agelaius phoeniceus*) of the North American prairies (names and taxonomy after AOU Checklist, 1983, for North American species and Gruson, 1976, for African species). The quelea is a sparrow-sized bird in the family Ploceidae which includes a great number of pest species, most notably *Passer* spp., *Ploceus* spp., *Quelea* spp. and *Euplectes* spp., all of which likely originated in grassland Africa. Redwings are in the family Emberizidae, subfamily Icterinae which includes two other important North American pest birds, the common grackle (*Quiscalus quiscula*) and the yellow-headed blackbird (*Xanthocephalus xanthocephalus*). These three blackbird species often flock together. Other major bird pest species are listed by Dyer and Ward (1977, Table 7.1).

Quelea can be an important constraint to sorghum and millet production in semi-arid areas of sub-Saharan Africa where a single rain-fed crop per year is produced. They also damage ripening rice and wheat. Destruction of nesting and roosting aggregations with pesticides is the most widely practised means of control. This can be effective when directed against aggregations that are doing damage or are likely to do so, but it has not been effective in long-term population reduction (Ward, 1973, 1979; Jones, 1980). A principal disadvantage of using pesticides for quelea control is the potential destruction of non-target birds.

Quelea research was intensified in the 1970s through programmes by the United Nations Food and Agriculture Organization (FAO) (Jackson and Allan, 1989) and American, British, French and German (GTZ, 1987) bilateral projects. Crook and Ward (1968) describe early quelea research. Studies have revealed that damage is localized and that there is considerable variability among localities in the spatial and temporal patterns of quelea movements. In order to develop localized control strategies, the seasonal patterns of quelea movement and nesting within an area must be understood.

Redwings damage ripening maize and sunflower in late summer and autumn in Canada and the United States. In general, damage is concentrated around marsh roosting sites where the birds gather after the breeding season and during migration. Destruction of roosting birds with pesticides has not been considered practical, due to adverse public opinion attending the killing of birds and to the potential for environmental contamination. Scientists, rather, have worked on developing techniques to disperse damage and thereby dilute its impact. A variety of frightening devices, chemical repellents, less preferred crop varieties and alternative cultural practices have been evaluated. As yet, no single technique has proved to be the solution. This is due, in part, to the unforeseen complexities associated with flocking, feeding choices and migration.

The first step toward efficient problem-solving is to understand the behaviour and ecology of the pest as it relates to the damage. This information will allow selection of appropriate control methods. Secondly, determining the spatial and temporal distribution of the pest birds in relation to crop damage permits developing a strategy for the most effective use of control methods. Refer to Dyer and Ward (1977) for a discussion of research strategies for bird pest problems.

This review compares the flocking and migratory behaviours of quelea and redwings in the context of agricultural damage. The implications of this basic information for control strategy are then examined. The spatial and temporal pattern of damage varies with local circumstances, and therefore the approach to control can vary as well (e.g. Elliott, 1979). To illustrate the situation-specific nature of these problems and of their solutions, this treatment will focus on two cases for which information is available: (1) quelea damage to lowland sorghum in the Awash River Basin of Ethiopia: and (2) redwing damage to ripening sunflower in the north-central United States. These examples contrast the two principal approaches currently used in bird control, population reduction and dispersion of damage by frightening or repelling the birds.

Flocking

Flocking is common to many species of birds: the term is used here to mean any aggregation of conspecifics. These aggregations are usually associated with roosting, feeding, nesting or migration. Flocks can be spectacular for their numbers and their behavioural displays (*Figure 1*). These aggregations are the subject of growing scientific interest. For both quelea and redwings, flocking seems to be tied closely to seasonal movements.

ROOSTS

Sites

Night roosts seem to be the underlying aggregation from which flightlines, feeding flocks, daytime roosts and nesting colonies arise. These roosts form at sunset and disperse at dawn. Quelea prefer low, dense patches of thornbush (e.g. *Acacia* spp.), but also commonly roost in marshes (*Typha* spp. and *Phragmites* spp.) and in sugarcane (*Saccharum* spp.), normally concentrating in areas of 10 ha or less (GTZ, 1987). Similarly, redwings prefer dense vegetation over water, usually in marshes or swamps (Meanley, 1965). Presumably, such vegetation allows for the very high densities of birds that characterize the roosts of both species, and possibly for flock interaction through the unobstructed detection of arriving or departing flocks. Vegetation characteristics seem to be an important criterion for roost-site selection (Lyon and Caccamise, 1981) as both species will fly long distances between feeding and roosting sites. Return trips of 60 km are not uncommon, and up to 160 km return trips have been observed for both

Figure 1. Flock of red-billed quelea. *Quelea quelea*. feeding in an African grain field (photo by M-T Elliott and courtesy of FAO).

species (Meanley. 1965: Jaeger. personal observation). Generally. however. feeding is concentrated nearer the roost. Traditional roosting sites are used year after year if conditions allow (Besser. De Grazio and Guarino. 1983: Jaeger *et al.*. 1986). These are frequently shared with other grain-eating bird species. commonly other ploceids and doves (*Streptopelia* spp.) in the case of quelea. and other icterines and European starlings (*Sturnus vulgaris*) in the case of redwings.

Seasonality

Night roosts are transient and variable in character. Site location. size. and sex and age composition of the birds depend on the season. the local pattern of migration and breeding. and on the availability of food in the late dry season for quelea and in winter for redwings. Quelea migrations are determined by the seasonal movement of the rainfront (Ward. 1971) which oscillates across the equator each year. resulting in a single rainy season with a prolonged dry season at the northern and southern extremes and bimodal rains near the equator (*see* Brown. Urban and Newman. 1982. for a description of the Inter-Tropical Convergence Zone). According to Ward's (1971) model. quelea begin their migration in response to the onset of the rains when the grass seeds upon which they have been feeding germinate. Movement is in the direction opposite to that of the rainfront. the distance depending on where concentrations of newly seeding grasses are to be found ('early rains migration'). Where suitable conditions are encountered those

quelea physiologically ready to breed will do so. Those not yet in breeding condition remain in that general area for approximately 6 weeks. or until conditions prompt the return movement ('breeding migration'). The early nesting adults can also follow behind the rainfront and rebreed ('itinerant breeding'). eventually completing the migration in the early dry season where it began (Jaeger *et al.*, 1986). Migrations will therefore vary in direction. distance and timing depending on the location of the dry-season concentrations of quelea in relation to the equator and on the local distribution of suitable habitat.

In addition to being localized. quelea migration within an area can be fragmented. that is. involving more than one group as opposed to a single massed movement (Jaeger *et al.*. 1986; GTZ. 1987). Individual groups form night roosts throughout the year. The largest roosts seem to be in the order of 10^6 birds and are associated with the formation or completion of nesting in areas where more than one colony was established. The smallest roosts (10^4) occur early in the dry season when food is widespread. At this time it is not uncommon to find two or more roosts in close proximity. As the dry season progresses and food becomes more patchily distributed. roosts tend to coalesce (Ward. 1965a; Jaeger. Erickson and Jaeger. 1979).

The continental pattern of redwing migration is relatively simple when compared to that of the quelea. being essentially north–south in direction and spring–autumn in timing (Dolbeer. 1978). From the local perspective. however. redwing migration is more fragmented than that of quelea in that breeding is more dispersed. The northward movement in spring (March–April) follows closely behind the retreating snow cover. whereas the autumn migration (August–December) is more of a casual drift southward spread over a longer period of time (Dolbeer. 1978; Besser. De Grazio and Guarino. 1983). Redwings tend to remain further north during mild winters than during more severe winters. Night roosts are used during the migration (e.g. Besser. De Grazio and Guarino. 1983) and throughout the winter (Bookhout and White. 1979; Heisterberg *et al.*. 1984; White. Dolbeer and Bookhout. 1985). A gradient for roost size and duration probably occurs where the largest ($10^6–10^7$) and most enduring roosts are in the southern part of the range in winter (Meanley. 1965). where both resident and migrant populations coalesce; while the smallest and most transient roosts occur at the northern extreme of the range as migrants begin grouping in the late summer and dispersing in the late spring. Breeding occurs between April and July. during which time nesting adults do not form communal night roosts. Flocking begins again in the late summer following breeding. coincident with the post-breeding (pre-basic) moult (Linz. Bolin and Cassel. 1983; Linz. 1986). Along the major migratory routes roost sizes are commonly of the order of $10^5–10^6$ individuals (Linz. Knittle and Cummings. 1988). Multiple roosts in the same area are not uncommon. particularly in the autumn when food is widely available (Jaeger *et al.*. 1983a). Large spring migratory roosts of the order of $10^6–10^7$ birds occur when spring storms halt the stream of migration (Otis. Knittle and Linz. 1986; Knittle *et al.*. 1987).

Segregation

Quelea and redwings both tend to be sexually segregated during migration. This segregation seems to be greater in the movement toward nesting areas. Consequently, pre-migratory and migratory roosts are often either predominantly male or female. Large roosts of adult males are more often observed than are large roosts of adult females or juveniles. Males of both species precede females in migration, suggesting that segregation may be initiated by males and may function in some way to influence the timing and/or route of movement and the choice of nesting areas. Juveniles or subadults are commonly observed flocking together, which probably reflects movement patterns different from those of adults.

In quelea, large, predominantly male roosts have been observed in the late dry season prior to the early rains migration (Ward, 1965b; Jaeger, Erickson and Jaeger, 1979). Greater female mortality due to competition with the larger males for a seasonally limited food resource has been suggested as the reason for this imbalance (Ward, 1965b). This explanation, however, does not account for the equal adult sex ratio during and following breeding. Predominantly female roosts of quelea were found in the Awash Basin of Ethiopia (*Figure 2*) in the late dry season but seemed smaller and more dispersed and therefore less conspicuous (Jaeger, Erickson and Jaeger, 1979). Plumage differences may promote segregation as males moult into breeding plumage in the late dry season, coincident with the appearance of large male roosts. Following the seasonal migration, males quickly moult out of breeding plumage.

Sexual segregation in quelea is also common following nesting (Jaeger *et al.*, 1986). Male feeding flocks and night roosts appear about midway through the 40-day nesting period. These night roosts are often formed outside of the nesting colony. Segregation precedes colony abandonment by the adults, following which they may complete the seasonal migration and breed a second time (Jaeger *et al.*, 1986). Both sexes presumably abandon colonies at the same time, usually leaving behind a large percentage of the juveniles who often remain in the vicinity of their colony site for days or even weeks. These juvenile flocks can remain segregated from adults throughout the juvenile period of approximately 4 months post-fledging, until completion of the post-juvenal moult (first pre-basic); possibly the same birds can remain together longer (Jaeger, Erickson and Jaeger, 1979).

For redwings, sexual segregation is common outside the breeding season (e.g. Smith and Bird, 1969), being particularly evident in migratory and winter roosts. For example, a large spring migratory roost regularly occurs in 285 ha of cattail (*Typha* sp.) marsh along the Missouri River at Squaw Creek National Wildlife Refuge (*Figure 3*). Millions of redwings use this roost *en route* north. Roughly 16 million blackbirds roosted here in mid-March 1982, 92% of which were male redwings (Knittle *et al.*, 1987). Numbers of blackbirds and turnover rate at this roost probably depend on the persistence of winter conditions. Early in the migration the roost is almost exclusively male in composition, and toward the end of the migration
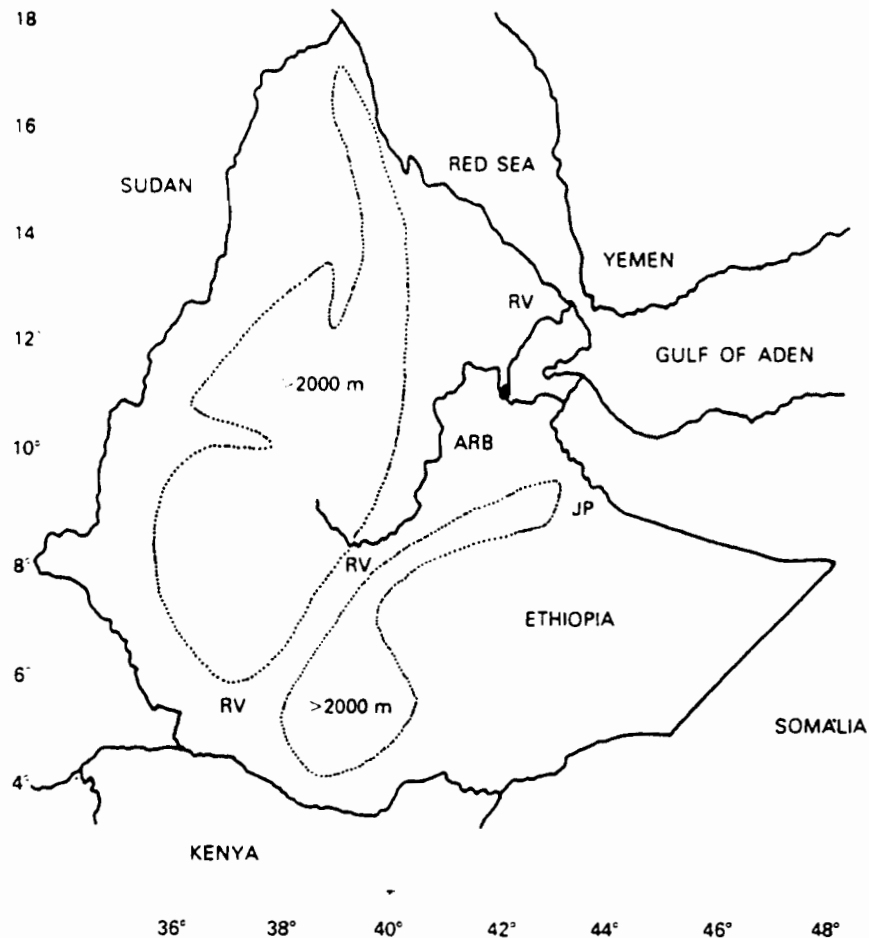
Figure 2. The Ethiopian Rift Valley including the Awash River Basin. ARB = Awash River Basin: JP = Jijiga Plain: RV = Rift Valley: > 2000 m = highlands above 2000 m elevation.

predominantly female. At times both sexes occur in large numbers yet have been observed to remain segregated while roosting, each occupying a different area of the roost (M. M. Jaeger, personal observation). Meanley (1965, p. 226) has suggested that sexual segregation occurs in all redwing roosts and is the result of '(1) birds feeding in segregated flocks during the day and returning to the roost in the same way; (2) flocks of birds of one species or one sex returning to a favorite section of the roost each evening; and (3) stratification within the roost.' Sexual dimorphism and male dominance (Weatherhead and Hoysak, 1984) may also promote segregation. Sexual segregation is also common in non-migratory resident redwings (Orians, 1961a; Meanley, 1965).

Evidence for segregation of age groups of redwings comes from ring recoveries (Dolbeer, 1982) and morphological comparisons of samples from

Figure 3. The central United States, illustrating the main corridor of migration of red-winged blackbirds. *Agelaius phoeniceus*, that damage ripening sunflower in the Dakotas and Minnesota (after Besser, De Grazio and Guarino, 1983). SC = Squaw Creek National Wildlife Refuge, the traditional site of a large spring migratory roost; SL = Sand Lake National Wildlife Refuge, the traditional site of large autumn migratory roosts; s = sunflower-growing area; m = maize-growing area; r = rice-growing area.

winter roosts (James *et al.*, 1984). Results suggest a differential migration among sex and age groups whereby adult males (referred to as after-hatching-year or AHY males) are generally found overwintering further north than hatching-year (HY) males, which in turn overwinter further north than females. Differential migration implies that AHY male redwings might be most prevalent at the Squaw Creek roost early in the spring migration, followed sequentially by HY males and females. Plumage differences may help maintain segregation through recognition of and attraction to familiar

types (Whitfield, 1987). Intraspecific segregation associated with migration has been reported in a variety of other species (*see* Howell, 1953; Myers, 1981; Ketterson and Nolan, 1985).

Morphological segregation may also result from the clinal gradient in body size where larger birds breed further north and west (Power, 1970). The cline is maintained by birds returning to the same breeding grounds each year (Dolbeer, 1978; Beletsky and Orians, 1987). As the timing of breeding varies with latitude, and as redwings tend to return to the same general wintering grounds (James *et al.*, 1984), those birds breeding in the same areas may well migrate at the same time, resulting in a degree of morphological segregation within or among winter/spring roosts.

Flock cohesion

Segregated flocking, differential migration in both time and space, and fidelity to nesting (Nero, 1956; Searcy, 1979; Jaeger *et al.*, 1986) and wintering areas suggest the possibility of long-term flock cohesion for both species. In Ethiopia, quelea marked together in nesting colonies with aerially applied fluorescent particles have been recovered together following migration (Jaeger *et al.*, 1986) and, in southern Africa, quelea ringed together have been recovered together many months later and hundreds of kilometres away (P. Jones, personal communication). For redwings, grouped sightings of birds tagged together with similarly colour-coded leg streamers and grouped recoveries of birds ringed together suggest long-term flock cohesion. In one instance, five AHY males with white leg-streamers were seen (two of them side by side) in a flightline of redwings entering a night roost near Squaw Creek in March 1982 (Jaeger, personal observation). These birds had been tagged a year earlier at a winter roost 520 km to the south. An outstanding example of a grouped recovery of redwings is of two AHY males ringed together in December 1964 in the state of New York and recovered nearly 1100 km to the north in Prince Edward Island, Canada, on successive days in April 1968 (unpublished, US Fish and Wildlife Service, Laurel, MD). We assume that the probability of this happening due to independent movements of the two birds is remote, particularly as redwing breeding is dispersed over a large area (Stewart, 1977; Dolbeer, 1978; Meanley and Dolbeer, 1978). If long-term flock cohesion occurs in redwings, then the size of the basic flock is probably small, consisting of either the males or females that breed in a particular marsh or in nearby marshes. For quelea, the basic flock size is probably larger since they breed in large colonies.

FEEDING FLOCKS

Flightlines

Flightlines occur when flocks moving in the same direction fall into line forming a more-or-less continuous stream of birds which can stretch over

many kilometres (*Figure 4*). These are usually associated with roost dispersal
in the morning and roost formation in the evening. For example, an evening
flightline of quelea *en route* to a roost passed for 45 minutes in a line that
contained an estimated 120 000 birds, or about 44 passing per second in a
space roughly $10 \times 10 \times 20$ m (M. M. Jaeger, personal observation).
Redwings seem to form continuous, unbroken flightlines more often than
do quelea. This may be because flightlines are associated with migration,
functioning as a mechanism for onward movement, and the time over which
quelea migrate is relatively brief. Flightlines of redwings are sometimes seen
to depart migratory roosts in the morning and leave the area even when
there is an abundance of ripening cereals near the roost. The size of these
flightlines can change daily, possibly reflecting the onward migration of part
of the roost or the arrival of new birds. Roost turnover has been measured
by Otis, Knittle and Linz (1986). Flightlines of both quelea and redwings
are characterized by an undulating movement (*Figure 4*) possibly making a
more conspicuous display for attracting conspecifics (Ward and Zahavi,
1973), or affording the birds a greater opportunity to see ahead when
cresting and thereby to learn landmarks along the route. Traditional paths
of flightlines have been noted for redwings using the same migratory roost
size (J. Besser, personal communication).

Feeding flocks usually begin breaking away from the flightline when food
is encountered. Generally, large numbers of birds stop briefly to feed, before
moving on to feed again (*Figure 1*). It is in the vicinity of the roost that
crop damage is most severe. During this morning exodus, flocks disperse
from the path of the flightline, some remaining behind at each stopover

Figure 4.   Flightline of quelea returning in the evening to their primary roost (photo by M. M.
Jaeger).

while others continue to fly on. The pattern of this dispersal seems to be related to that of food, water and daytime roosting sites. Feeding flocks, therefore, tend to become more scattered during the autumn migration in the case of redwings, and during the early dry season for quelea, when food is widespread. The return of feeding flocks to the roost in the evening is usually more fragmented and spread over a longer period of time than is departure in the morning (Meanley, 1965) and is probably related to the pattern of daytime scatter.

Staging behaviour

Roost formation and dispersal are usually preceded by an activity that has been termed 'staging behaviour'. This is common for many species (*see* Wynne-Edwards, 1972, p. 286) including quelea and redwings, and is most prominent in the evening. It is characterized by flocks settling in or near the roost only briefly before taking off again and resettling elsewhere, often at a staging site outside the roost near trees, water or food to where other flocks are attracted (GTZ, 1987). During staging, streams of birds often fly past one another in opposite directions. This reshuffling or intermixing of flocks may continue for 30 min or more. Before finally settling, whole areas of the roost may rise, shift position and resettle. Little is known about the function of this activity. It may serve as a display to advertise the roost and attract nearby birds (Wynne-Edwards, 1972; Ward and Zahavi, 1973). Weatherhead (1983) has suggested that staging functions in the establishment of a flock dominance hierarchy within the roost whereby dominant flocks obtain the preferred locations that are less vulnerable to predators.

Flock size

From the previous discussion it follows that the size, number and distribution of feeding flocks will vary with roost size, the spatial distribution of food in relation to the roost, and the time of day. The largest concentrations of feeding birds are those associated with large flightlines as they depart the roost in the morning. The potential for localized damage by flightlines of redwings can be substantial. Feeding aggregations of up to 10 000 redwings are not uncommon along flightlines during migration (Dyer, 1967). Besser (1978) states: 'On several occasions, flightlines of approximately one-quarter million birds leaving or entering roosts have been observed to pass over a single sunflower field, different flocks entering and leaving the field simultaneously. A population estimated at 62 000 blackbirds was once observed in a single 16-ha field near Hope, North Dakota.' Adverse weather can also cause large feeding flocks by forcing birds to remain close to the roost throughout the day (Hamilton and Gilbert, 1969; Dolbeer *et al.*, 1978). The most common size of redwing and quelea feeding flocks, however, is in the order of 10^2-10^3 birds. As previously suggested, there may be a basic flock unit for both species which remains together throughout the day and possibly for longer. This would likely be small in size, especially for redwings,

since small flocks are commonly observed. Orians (1961a), for instance, reported flock sizes of resident redwings in California to average about 10 individuals. It has also been suggested for other species that large flocks are 'loosely organized assemblages of smaller groups which behave more as coordinated units' (Miller and Stephen, 1966).

Searching behaviour

Flock feeding in birds is generally assumed to be an adaptation to optimize feeding efficiency where food is patchily distributed in time and/or space (Pulliam and Millikan, 1982). The mechanism by which optimization is achieved will vary with the species and the feeding context: for instance, the search strategy of great tits (*Parus major*) feeding in small patches of forest canopy may benefit from observing the type and location of prey taken by nearby individuals (Thompson, Vertinsky and Krebs, 1974). The situation is different for quelea and redwings which are principally granivorous in the non-breeding season, feeding on relatively few food types (Ward, 1965a: Hintz and Dyer, 1970; Erickson, 1979; Linz *et al.*, 1984) but searching for dense patches of food over much larger areas. Here it is difficult to see how flock searching can be more efficient than individual searching. Scattered individuals must be able to search a greater area than grouped individuals. The advantage of flock feeding may not be in searching *per se*, but in signalling the position of food whereby successful flocks (those feeding) attract nearby flocks; if the food patch is rich, flocks accumulate, become more conspicuous and thus attract more distant flocks. This attraction to feeding birds has been termed 'local enhancement' (Thorpe, 1956; Hinde, 1959) and is a commonly observed phenomenon in both quelea (Crook, 1960; Ward, 1965a; GTZ, 1987) and redwings. Theoretically, this flocking behaviour would benefit all individuals, assuming all flocks have an equal probability of finding food, and all individuals in a flock have an equal opportunity to participate in feeding. It would seem that for local enhancement to work efficiently, the searching flocks would have to maintain contact with one another either by co-ordinated movements or by concentrating their search within a small-enough area.

The use of a communal roost as an 'information-centre' for the location of food patches (Ward and Zahavi, 1973) is one possible way to co-ordinate flock searching. Feeding flocks return to the primary roost in the evening or secondary roosts during the day [also referred to as day roosts or 'diurnal activity centers' by Caccamise and Morrison (1986)]. Successful flocks later return to the general area in which they have been feeding, drawing unsuccessful flocks along with them. All flocks then search the patch and all benefit from local enhancement. This model assumes that food patches themselves are not homogeneous, but are a cluster of smaller patches, and that they are generally large enough to be reused. These are reasonable assumptions for both quelea and redwings. In semi-arid grassland Africa, for instance, heavy rainfall is localized and may drench only relatively small areas at one time, covering only a few hundred or thousand hectares within

which seed production will be associated with the pattern of drainage. Seasonal drainages and flooding patterns can result in large traditional (predictable) patches of grass growth.

In order to reuse feeding sites efficiently, birds must be able to find them again. How do far-ranging flocks do this? Presumably they are able to learn the location by following a general direction and by orienting on a succession of landmarks (Meanley, 1965). This could be a relatively easy learning task when following a river or a highway, which both quelea and redwings will do, but it can become more complex where prominent landmarks do not occur near the food patch. We suggest that behavioural mechanisms to facilitate learning the locations of daily feeding, drinking and roosting sites are important to species such as quelea and redwings that range far in their daily flights. These mechanisms could be particularly important during migration where there are new foraging situations to learn. Flocking may be one mechanism which facilitates spatial learning by pooling the experience of the individuals of the flock. This assumes that some individuals in the flock will be more familiar with each of the decision points along a route and that birds with less experience will follow. There is experimental support for this in quelea where naïve birds tended to follow experienced birds to a food source (DeGroot, 1980). DeGroot suggested that the very synchronous flock behaviour of quelea (which includes turning in flight) is a following response that may have been adapted as a mechanism for exchanging information. By extension, when the flock comes within sight of other flocks *en route* to the same location, their tendency will be to follow the general flow. The use of traditional nesting areas, roost sites, flightline paths and feeding areas will simplify the learning task. Group cohesion may be an important means of maintaining the integrity of collective group information about directions (Jaeger *et al.*, 1986).

Frequent sampling of a large area within the range of the roost would facilitate learning the locations of a variety of food sources and secondary roosting sites. Both species seem to do this in cropping areas even where food is abundant and widespread, feeding at several different locations during the day, often far from the roost. Such behaviour may seem inefficient in terms of energy use and is difficult to understand in the context of short-term strategies for foraging optimization (Katz, 1974). By frequent sampling, birds are able to select particular fields as the crops in them become susceptible. For cereals this usually occurs during the milk or soft-dough stage which the birds may prefer (Ward, 1965a; Meanley, 1971). probably because the seeds are moist and easier to extract. In addition to the crop type and its stage of development, birds quickly learn to distinguish and to show preferences for particular varieties of a crop; for example, quelea and redwings prefer low-tanning sorghums (Bullard *et al.*, 1980). Experimental studies support the above observations on the ability of redwings to sample their environment, to use locational and visual cues while foraging, and quickly to discover food preferences and to make changes in foraging strategy (Alcock, 1973). Studies of flock feeding behaviour in the field also indicate discriminant feeding (Dyer, 1967).

Secondary roosts

Secondary roosts, or day roosts, are used by both quelea and redwings as resting sites between bouts of feeding; they can be important as foci for crop damage. During the non-breeding season, the pattern of feeding tends to be bimodal with the most sustained or frequent bouts associated with entering and exiting the primary night roost (Hintz and Dyer, 1970; Ward, 1978; GTZ, 1987). Throughout much of the day, flocks are usually found close to a secondary roost from which they periodically forage for short periods. There may be many secondary roosts scattered within range of the night roost, each containing several thousand birds. These are often in the same type of vegetation used for the primary roost, usually near food and water. Birds feeding near the primary roost will often return there during the day. It is not uncommon for quelea to form secondary roosts in sorghum fields where they can do extensive damage. For example, quelea were observed to destroy completely a 40-hectare sorghum field in Ethiopia in which they were roosting (M. M. Jaeger, personal observation); most of the kernels were not consumed but appeared to have been picked and dropped on the ground. Redwings will also use maize or sunflower fields as secondary roosts, particularly if irrigated. Both species seem attracted to areas within fields where plants are relatively dense or weed-filled (Bollinger and Caslick, 1985; Luder, 1985); presumably these areas offer cover from predators.

A secondary roost site may be used repeatedly by a flock and serve as a regular, long-term 'base of operations' (Caccamise and Morrison, 1986). Resident starlings, for instance, showed greater fidelity to their 'diurnal activity centers' than to seasonal communal roosts (Morrison and Caccamise, 1985). Flocks of quelea or redwings may establish similar reference points in order to simplify learning long-range routes, for information exchange among flocks as earlier suggested, or possibly as a site for flock members to regroup after becoming separated and thereby facilitating group cohesion. Fidelity to particular feeding areas may help to ensure flock dispersal relative to the primary roost and reduce the risks of overflocking (Clark and Mangel, 1984).

NESTING COLONIES

Quelea

Quelea nest in large, dense colonies which are the principal targets of control operations to reduce their numbers (GTZ, 1987). These colonies are usually found in dense thornbush (*Figure 5*), most often in those species with small, recurved thorns (e.g. *A. mellifera*) that make penetration by predators especially difficult (Disney and Marshall, 1956; Morel, Morel and Bourliere, 1957; Ward, 1965c). Colony size and nest density vary widely. In eastern Africa, successfully completed colonies have been found that ranged in size from 0.25 to 220 ha. The average size is about 20 ha (Ward, 1965c; Thiollay, 1978; Erickson, Jaeger and Bruggers, 1989). Nest densities ranged from 2500 nests ha^{-1} in scattered *A. mellifera* to 145 000 nests ha^{-1} in dense

Figure 5. Quelea nesting colony in thornbush (*Acacia* spp.) (photo by M. M. Jaeger).

A. nilotica among 12 colonies sampled in Ethiopia and Kenya (Erickson, Jaeger and Bruggers, 1989). The total number of active nests in these colonies averaged about 300 000 per colony, which represented an average of 1.3 million birds per colony based on one pair of adults and an average of 2.8 fledglings per nest. In addition, these colonies were found in clusters, usually of two or three colonies within a radius of roughly 10 km. Nesting is synchronous within but not among the colonies in a group. Present evidence suggests that colonies within a group form successively as birds in an area become ready to breed. A cluster of colonies represents, in effect, a supercolony.

Colonial breeding is common among granivorous species and is believed to be an adaptation to an uneven or patchy distribution of food (Wiens and Johnston, 1977). Resources needed for nesting are clumped in both time and space. This is especially true for quelea nesting in semi-arid Africa where the combination of seeding grasses, insects, water, nesting vegetation and green grass for nest construction necessary for breeding (Ward, 1965c) is short-lived at any particular site. In addition, there can be year-to-year differences in availability of nesting habitat due to the frequent occurrence of localized drought. Itinerant breeding and the regular use of traditional nesting areas have been suggested as further adaptations to the patchy distribution of nesting habitat (Ward, 1971; Jaeger *et al.*, 1986).
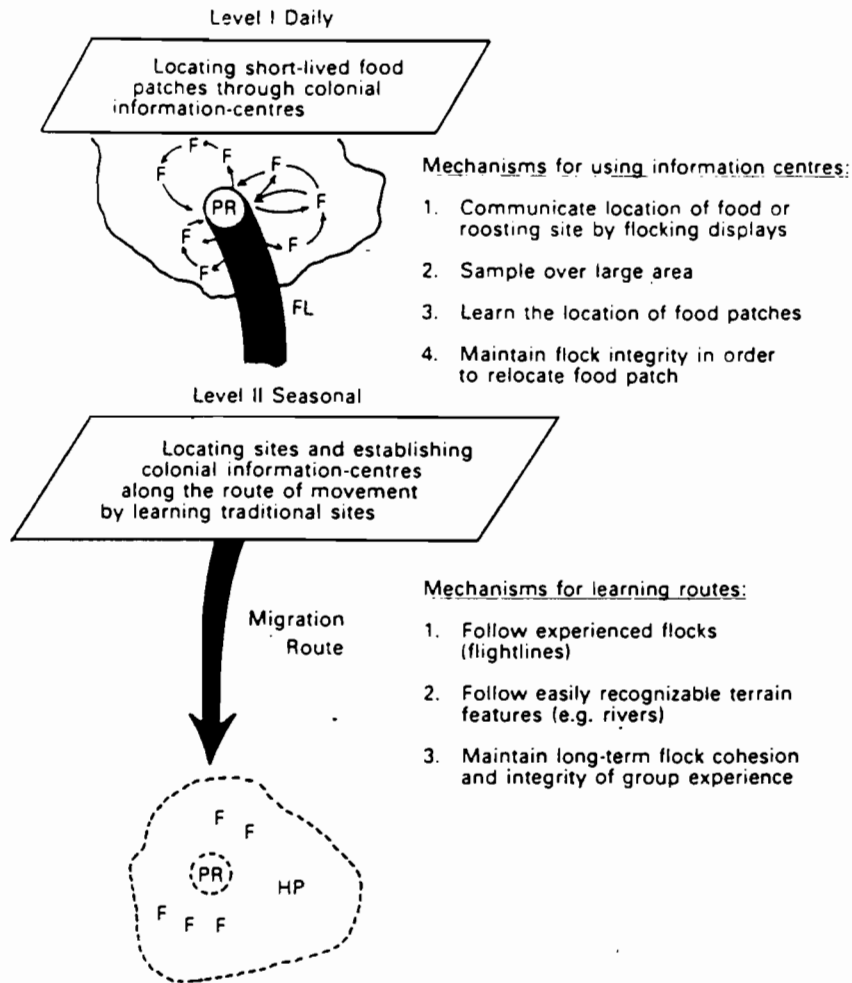
Redwings

Redwings nest either in individual polygynous units or in groups of units. Redwing nesting 'colonies' differ greatly from those of quelea in bird

numbers and density. Where redwings nest together in a marsh. group size is relatively small. nest density relatively low. and synchrony among nests relatively less (Orians, 1961b). The reasons for this are that redwings maintain much larger breeding territories than quelea: they are also polygynous and occasionally are multi-brooded on the same territories. Group size is therefore largely determined by the size of the marsh: and these are frequently small. sometimes an isolated clump of cattail with a single territory. Orians (1961a) reported a density of 10.1 territories per hectare in marsh habitat. Monahan and Cameron (1982) found 46 males holding territories in 2.9 ha of marsh (15.9 territories ha^{-1}) which contained 176 active nests (3.8 females/male) during the week of peak nesting. The largest nesting aggregations for redwings are probably of the order of 10^5 adults with 2–3 fledglings per nest. The icterine with the largest and most dense nesting colonies is the closely related tricolored blackbird (*A. tricolor*). It has a very restricted distribution. being confined largely to the Great Valley of California (Neff, 1937; Orians, 1961a). Its colonies can be of the order of 10^5 nests in a nesting habitat similar to that used by redwings (Orians, 1961a).

Redwing nesting is more evenly distributed within its range than is that of quelea. In addition to nesting in wetlands. redwings also nest in a variety of upland habitats (Dyer *et al.*, 1973; Besser *et al.*, 1987). The greater scatter of redwing nesting reflects a basic difference in the distribution of food consumed. Redwings are more insectivorous while breeding than are quelea (Ward, 1965a,c; Hintz and Dyer, 1970; Erickson, 1979). and insects are more widely scattered in time and space during the North American summer than they are following the rains on the savannahs of semi-arid Africa (Sinclair, 1978).

SIGNIFICANCE OF FLOCKING TO EXPLOITATION OF A HETEROGENEOUS ENVIRONMENT

The preceding discussion of flock types suggests (1) that an important function of flocking in both quelea and redwings is in exploiting resources that are clumped in both time and space along seasonal routes of movement; and (2) that the problem of locating clumped resources can occur at two levels of time and space. within the range of a migratory roost/nesting colony (Level I) and between it and the subsequent roost/nesting colony (Level II). *Figure 6* illustrates the functions flocking may have in locating resources at each of these levels. Ward and Zahavi (1973) postulated that quelea aggregations served as short-term information centres about the location of food clumps within range of the roost or nesting colony (Level I). The information-centre hypothesis has since received considerable attention (Emlen and Demong, 1975; DeGroot, 1980; Weatherhead, 1983; Brown, 1986; Elgar and Harvey, 1987). Jaeger *et al.* (1986) suggested that colonial nesting may also provide for longer-term information use on the location and timing of subsequent nesting opportunities at distant sites (Level II). According to this model:

Level I Daily

Locating short-lived food
patches through colonial
information-centres

Mechanisms for using information centres:

1. Communicate location of food or
   roosting site by flocking displays

2. Sample over large area

3. Learn the location of food patches

4. Maintain flock integrity in order
   to relocate food patch

Level II Seasonal

Locating sites and establishing
colonial information-centres
along the route of movement
by learning traditional sites

Mechanisms for learning routes:

1. Follow experienced flocks
   (flightlines)

2. Follow easily recognizable terrain
   features (e.g. rivers)

3. Maintain long-term flock cohesion
   and integrity of group experience

Migration
Route

Figure 6. Proposed function of colonial aggregations of quelea and redwings, to serve as information centres about the location of clumped resources at two levels in time: present and future. PR = Primary roost; F = food patch; FL = flightline; HP = habitat patch.

1. collective experience within a group of birds about the location and timing of distant resources is more complete and reliable than is individual experience (Clark and Mangel, 1984), particularly as route complexity increases, e.g. over longer distances or greater time intervals; and

2. long-term flock cohesion facilitates the use of group experience.

Furthermore, the re-use of traditional roosting and nesting sites could maintain dispersal among groups and reduce the impact of locally unfavourable conditions such as drought. This is referred to as 'spreading the risk' by Den Boer (1968).

What is the significance of flock functions to control strategies for quelea and redwings? A number of general predictions can be made from the preceding discussion. At Level I: (1) damage in the vicinity of a roost can be concentrated and severe; and (2) the focus of concentration can change rapidly over a large area. so that if vulnerable crops are widespread around a roost then protection of the crop (e.g. with chemical repellents or frightening devices) will have to be widespread. It then follows that roost destruction (e.g. with avicides or explosives) is likely to be more effective and economical than is widespread protection infields. In the context of seasonal movements (Level II): (1) damage will tend to occur around the same major roosts or nesting colonies each year; and (2) in a heterogeneous environment the spatial and temporal pattern of damage will vary with location. If the birds which form traditional roosts move together (group cohesion). then the potential exists for the selective destruction of prior aggregations before they arrive in cropping areas. Furthermore. if multiple roosts occur in the same general cropping area and are composed of birds that flocked together earlier in the season. then it may be possible to identify and destroy the source aggregation before it breaks apart. It follows that appropriate control strategies will vary with local circumstances. These points will be illustrated in the two following descriptions of bird control strategies used in specific situations in Africa and North America.

Crop damage and control

In this section we describe quelea damage to lowland sorghum in the Ethiopian Rift Valley. and redwing damage to sunflower in the north-central United States. Damage patterns are described in relation to the seasonal movements and flocking behaviour of each species. and the control efforts in each situation are contrasted.

ETHIOPIAN RIFT VALLEY

Quelea damage to lowland sorghum

Sorghum is the cereal traditionally grown at the lower elevations of Ethiopia (below 2000 m; *Figure 2*) where only a single. rain-fed crop is produced each year. and yields are often low due to sporadic rainfall. It is in these semi-arid drought-prone areas that quelea are most numerous (Urban and Brown. 1971; Jaeger and Erickson. 1980). Where quelea occur. damage can be severe and result in food shortage. Traditional methods of bird scaring have not been effective against large concentrations of quelea. Farmers often substitute maize for sorghum because quelea are unable to remove the husk from the ear. Maize. however. is generally less well suited to low rainfall. and consequently very poor yields can result. The impact of bird damage is probably greater here and in similar situations across the Sahel than elsewhere world-wide due to the very large flocks of quelea combined with otherwise poor yields of subsistence agriculture.

There are an estimated 500 000 ha of lowland sorghum planted each year in Ethiopia, almost exclusively on small farm holdings. This represents about one-half of the total amount of sorghum grown annually in Ethiopia (G. Brhane, personal communication). Most is clumped in river valleys or along the base of the escarpment. Approximately 60% is grown in the Ethiopian Rift Valley; of this an estimated 250 000 ha is in association with the Awash River Basin (*Figures 2* and 7) where surveys and control have
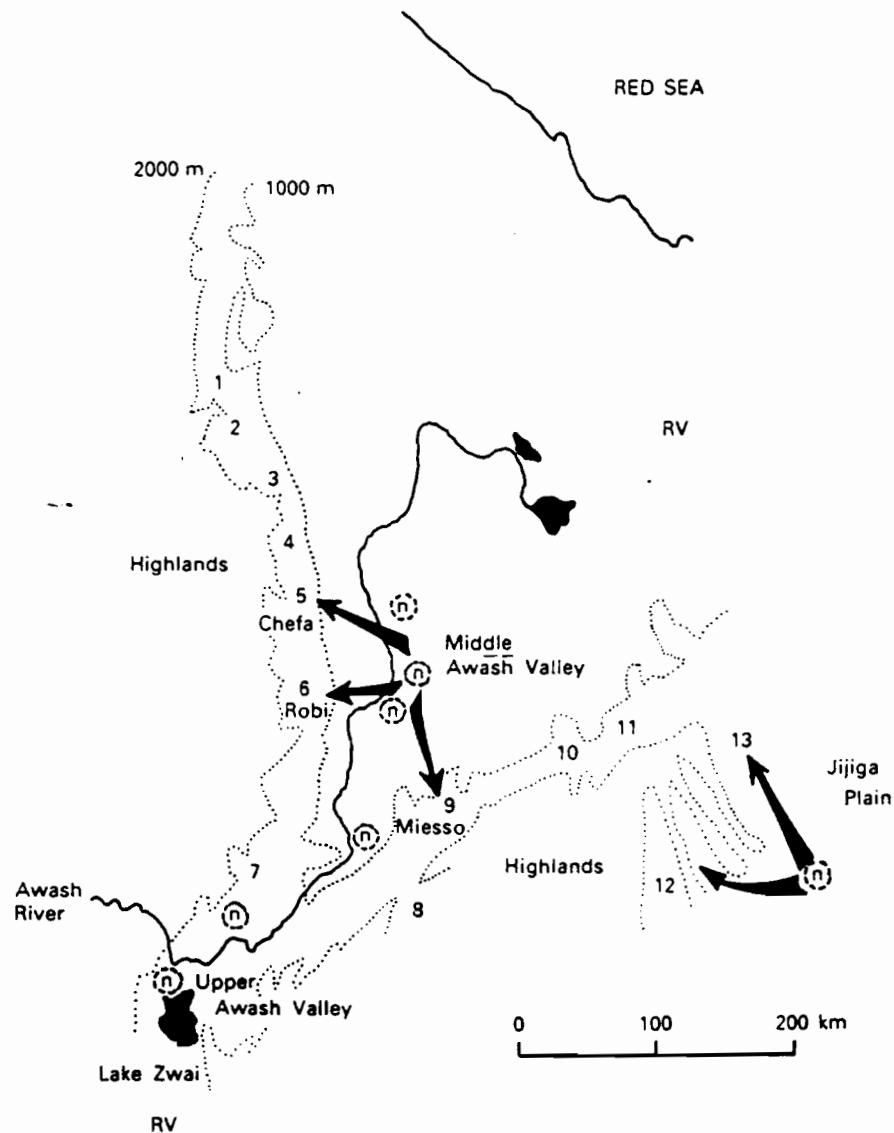
Figure 7. Major concentrations of lowland sorghum associated with the Awash River Basin and adjoining Jijiga Plain (1–13) in relation to the locations of traditional sites of quelea nesting (n) (after Jaeger and Erickson, 1980). Refer to *Table 1*. Arrows indicate the directions of post-nesting dispersal; RV = Rift Valley.

Table 1. Estimates of bird damage to sorghum in the major growing areas associated with the Awash Basin (1976–81)

Location†	Estimated area‡ (ha × 10³)	Bird damage (percentage loss)§						
		No control of nesting colonies				Control of nesting colonies		
		1975	1976	1977	1978	1979	1980	1981
Awash: 1 Kobo	15–30			(–)	(–)	1.2	4.9	2.8
2 Woldia	10–20					2.3	3.9	1.6
3 Ambassal	5–10						2.5	(–)
4 Bati	10–15		18.6*	(–)	1.5	1.0	2.4	0.9
5 Chefa	10–15			9.2*	0.6*	1.9	3.1*	2.6
6 Robi	10–20		10.3	16.1	3.1	3.5	8.1	4.7
7 Minjar/Welenchiti	5–10			(–)	2.8	(–)	1.3	0.8
8 Gelemso/Mechara	1–10	(+)	(+)		(–)	2.4	0.8	(–)
9 Miesso	20–30	(++)	13.3	(++)	0.6	(–)	(–)	1.2
10 Melka Jebdu	1–5				3.0			(–)
Jijiga: 11 Alemaya	20–65	(++)			(+)	(–)	(–)	0.1
12 Erer Valley	10–15	(++)			1.7	0.4	9.3*	1.5
13 Jijiga Plain	1–35		51.4**		3.2	9.3		2.4

(–) Qualitative estimate ≤5%; (+) qualitative estimate 5–10%; (++) qualitative estimate ≥10%.
* Local control of a single roost; ** local control of multiple roosts.
† Refer to Figure 7.
‡ Estimated range observed over period 1976–81. Low figures are the result of drought or civil disturbance.
§ See Jaeger and Erickson (1980) for method of damage assessment.

been focused (Jaeger, Erickson and Jaeger, 1979; Jaeger and Erickson, 1980; Jaeger *et al.*, 1986).

Preharvest damage assessments were made annually from 1976 through 1981 in the major sorghum-growing areas associated with the Awash River Basin (*Figure 7, Table 1*). Results indicated that annual losses within this system could be substantial, and that damage was clumped and tended to recur in the same areas each year (Jaeger and Erickson, 1980). Damage to the 80 000–100 000 ha surveyed in 1976 was estimated to be between 24 000 and 27 000 mT, or 27–30% of the expected yield of 1 mT ha⁻¹. These losses would have been even greater had it not been for the destruction of quelea roosts in two of the four areas sampled. The most serious losses occurred on the Jijiga Plain where an estimated 51% of 35 000 ha, or nearly 18 000 mT, was destroyed. The earlier-maturing sorghum here was completely destroyed. Quelea did not appear to have actually consumed all of this; much of the damage occurred at the milky stage when the kernels were punctured and left to dry out. There was also considerable wastage at later stages of maturity as evidenced by the litter of broken kernels on the ground. Damage in 1977 could be measured in only two of the sorghum areas, covering 25 000 to 35 000 ha, where losses were estimated to be from 3000 to 5000 mT, or 13% of the expected yield. Again, timely control of quelea roosts in one of the areas reduced damage. Losses from 1978 through 1981 were reduced through more effective control; this will be discussed later.

Overall losses to lowland sorghum in the Awash–Jijiga system may have reached about 40 000 mT annum⁻¹ under conditions favourable for sorghum cultivation and in the absence of any quelea control. This would have represented 16% of the expected yield from 250 000 ha, but less than 4% of that from the total of approximately 1 million ha of sorghum grown annually in Ethiopia; yields are greater in the highlands. Most of the country's grain production is in the highlands where wheat, barley, teff (*Eragrostus tef*) and maize are the principal cereals, and where bird damage is not a problem. Therefore, quelea damage to lowland sorghum in the Awash–Jijiga system, while substantial in itself, represented less than 1% of the total grain produced in Ethiopia.

It is difficult to make meaningful comparisons between levels of quelea damage in the Ethiopian Rift Valley and those elsewhere in Africa, due to the lack of similar information on both the amount and distribution of vulnerable crops and loss estimates over significantly large areas. Nevertheless, some generalizations can be made. First, the distribution of vulnerable crops is usually clumped. Secondly, quelea damage can be an annual problem and tends to be localized. Finally, losses to birds represent only a small part of total grain production in most countries. Exceptions, however, probably occur where sorghum or millet monocultures exist and where overall cereal production is low (Bruggers and Ruelle, 1981).

Seasonal distribution of quelea

Quelea damage to sorghum in the Awash–Jijiga system (*Figure 7*) occurred from August through November following the main rains (Jaeger and

Erickson. 1980). The timing of sorghum maturity varied with location. being earlier at lower elevations in the southeast (e.g. Jijiga) and later at higher elevations to the northwest (e.g. Chefa). resulting in a corresponding gradient in the onset of damage. In general. quelea were present in these cropping areas only during the period when ripening sorghum was available: this could be 6 weeks or more. depending on the spread of planting dates and differences between early- and late-maturing varieties. At Jijiga. for instance. damage began in mid-August in areas with early-maturing fields and continued into October in late-maturing patches.

Night roosts were widely scattered through the Awash–Jijiga system during the time of sorghum damage. This followed nesting and was the time when quelea numbers were at their annual high. There were two nesting areas from which these quelea had dispersed. The first nesting occurred in the northern Ogaden during June and July (*Figures* 7 and *8*). and this was the source of those quelea damaging sorghum on the Jijiga Plain and nearby areas beginning in August. Colony sites here were never found. but evidence suggested that nesting occurred near Jijiga. The very extensive damage that occurred on the Jijiga Plain in 1976 was caused by juvenile quelea. Five large night roosts of juveniles were found over a period of 6 weeks and destroyed by control operations. Adults from this June–July nesting in the northern Ogaden may migrate to the Awash Valley and nest a second time (Jaeger *et al.*, 1986). or alternatively may move to nearby sorghum-growing areas in adjacent Somalia. from where post-breeding adults have subsequently been collected.

The second nesting was from August through October in the Awash Valley and at Lake Zwai. where colonies were found annually from 1978 through 1981 (*Figure 8*). Known nesting sites extended over 300 km of the Awash Valley (*Figure* 7). Most colonies. however. were in semi-arid savannah along the middle Awash River below 1000 m elevation and well away from the sorghum-growing areas where damage would occur. In 1981. for example. 14 nesting colonies were found in the Awash Valley below 1000 m and two above this elevation near Lake Zwai. Nesting tended to be clumped in both time and space. with the earliest colonies being established in August to the north and the last colonies in late September or early October to the south near Lake Zwai. Evidence suggested that many of the adults in these colonies had nested earlier in the season. either at the southern end of the Ethiopian Rift during May and June (*Figure 8*) or in the northern Ogaden during June and July (Jaeger *et al.*, 1986). The breeding season ended with this second round of nesting in the Awash Valley. and quelea dispersed. led by the adults.

Roosts of adults first appeared in the adjacent sorghum-growing areas in late October and early November. There were three areas in particular where quelea were a perennial problem: Chefa. Robi and Miesso (*Table 1*. *Figure* 7). These were the major sorghum areas nearest to the main concentration of nesting colonies in the middle Awash Valley. To reach these sorghum areas following nesting. quelea had to cross between 50 and 100 km of dry bush land. where food could be scarce. Quelea. therefore.
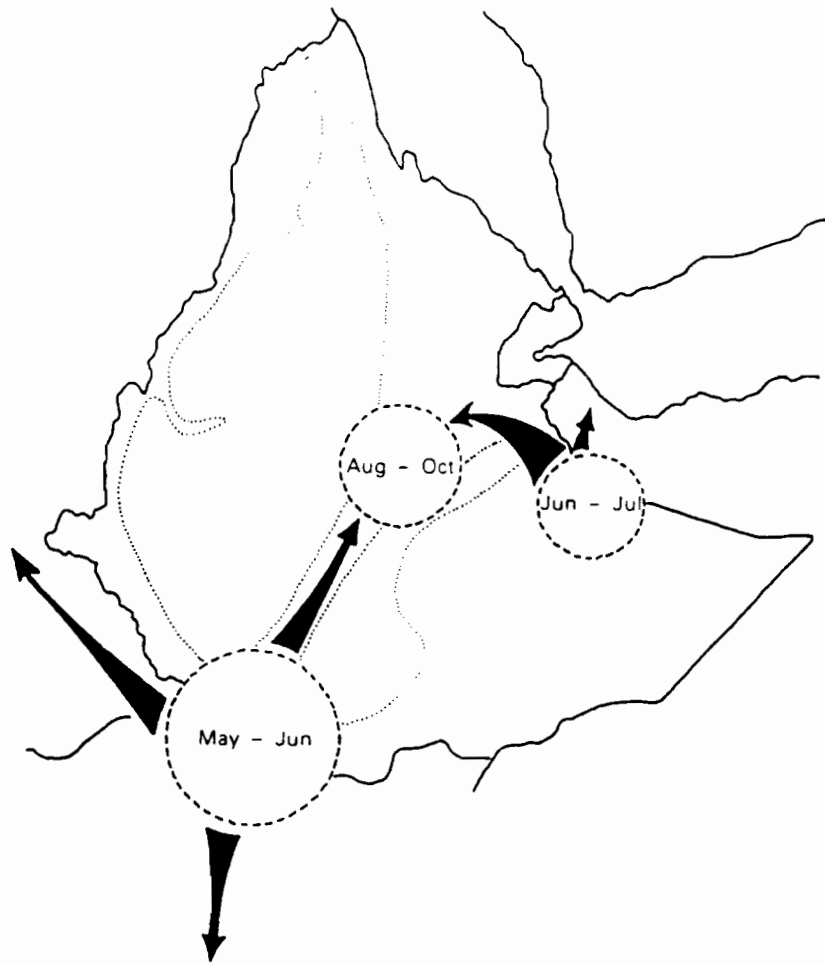
Figure 8. Locations and timing of quelea nesting in the Ethiopian Rift Valley and northern Ogaden, with the likely directions of post-nesting dispersal.

depart the middle Awash where grass seeds are seemingly available both at the time of colony dispersal and when the birds return later in the dry season. This seems to contradict Ward's (1965a) observation from northern Nigeria that quelea preferred the smaller seeds of wild grasses (Graminae) and damaged the larger cultivars only in their absence. He argued that quelea are forced to leave feeding areas at the time the seeds shatter and fall to the ground because the seeds drop into a tangle of grass stems and are unavailable to quelea until this annual grass is burned off or otherwise dries out and breaks down (Ward, 1965a). Erickson's (1979) study of foods eaten by quelea in different ecological zones of the Awash Valley suggested that seed density is a more important determinant of food preference than is size (within limits) or type, and that quelea may therefore prefer cultivated

sorghum where it is easier to obtain than wild seeds. Nesting is energetically demanding (Jones and Ward, 1979), and it may be advantageous for quelea to move to an abundant and dense food source following nesting in order to recover.

How do quelea locate these remote sorghum-growing areas at the time they become susceptible? Possibly they learn the locations and timing of these traditional sorghum-growing areas in the same way they seem to learn to use traditional nesting and roosting sites (Jaeger *et al.*, 1986). In the Awash Valley the three sorghum areas to which quelea seem to return regularly are each drained by a seasonal river which empties into the middle Awash River near the nesting sites; flocks may use these rivers as landmarks, following them to and from the sorghum-growing areas.

Quelea control

Spraying avicides.   Spraying roosting or nesting aggregations with avicides is the method of quelea control that has proven the most effective. Organophosphate insecticides, principally fenthion and parathion, are used for this purpose in Africa (*see* Schafer *et al.*, 1973, for acute LD_{50}; GTZ, 1987). Organophosphates disrupt nerve function at the synapses by interfering with the reaction between the neural transmitter acetylcholine and the enzyme cholinesterase which deactivates it (O'Brien, 1967). Spraying is usually done from a fixed-wing aircraft at dusk when most birds have returned to the roost for the night. The most effective technique is to drift a dense curtain of small spray droplets (< 100 μm in diameter) slowly across the target in a light wind at from 5 to 10 m above the vegetation, so that birds fly through the chemical. Effective spraying requires considerable preparation, including determining the timing of the birds' arrival and of the probable direction of the wind, familiarizing the pilot with the target so that he can time and position the spray runs efficiently, and positioning a ground crew at the target able to help direct the pilot. A carefully done control operation can kill almost 100% of the targeted birds. See GTZ (1987) for a more complete description of spraying quelea.

Developing a local strategy of population reduction.   The strategy for quelea control in the Ethiopian Rift Valley developed from one of destroying roosts that were doing damage (1976–77) to one of destroying nesting colonies in the Awash Valley before they dispersed to the sorghum-growing areas (1978–81) (Jaeger and Erickson, 1980). Annual damage assessments were used to compare the effectiveness of each strategy. Both strategies were selective, aimed at removing only those birds either causing damage or likely to do so, as opposed to general population reduction. Nesting colonies in the southern Rift Valley were not treated because levels of post-nesting damage to sorghum in that area did not justify it, and evidence suggested that post-nesting dispersal by adults was not exclusively to the north into the Awash Valley (*Figure 8*).

Damage to ripening sorghum bordering the Awash Valley dropped after 1977 to an annual average of 2% of the expected yield for the total area surveyed (*Table 1*). This drop coincided with the destruction of Awash nesting colonies. The effect of this control is best illustrated with the main problem areas of Chefa. Robi and Miesso. where the estimated damage was lower during the 4 years of nesting-colony control than during the 2 preceding years (*Figure 9*). Nesting colonies were found in the middle Awash Valley during each of these 4 years. the fewest being two colonies in 1980. when the rains failed over much of this area. and the most 14 in 1981. when rainfall was relatively high. Destruction of these colonies did not completely eliminate the damage. and local roost control was undertaken in two instances (*Table 1*). Reasons for this may have been that not all colonies were found. that the treated colonies were only partially destroyed. or that some birds did not breed due to localized drought as may have occurred in 1980. Damage was also low during these control years in the other areas surveyed in the Awash Basin (*Table 1*). but no pre-control damage estimates exist for comparison. Reduced damage at Jijiga was due to the almost complete absence of small farms after 1976. a result of the war with Somalia.

Controlling nesting colonies was more effective than controlling later roosts in the sorghum-growing areas because control could be completed
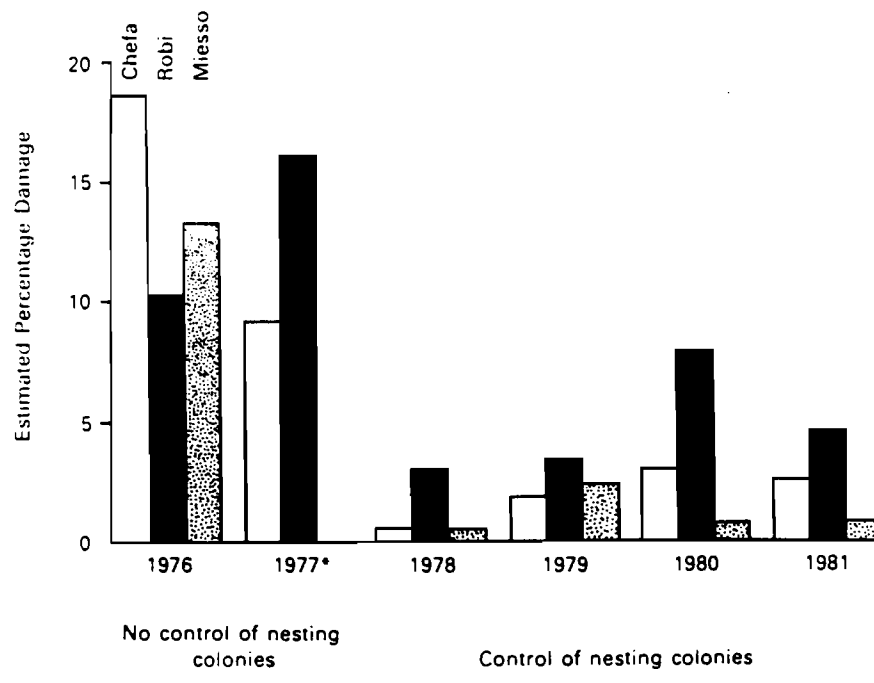

Figure 9. Estimated bird damage to preharvest sorghum at Chefa. Robi and Miesso (refer to *Table 1* and *Figure 7*) before (1976–77) and following (1978–81) annual control of quelea nesting colonies in the middle Awash River Valley. * No information available for Miesso.

before the onset of damage. Significant damage can occur in a sorghum area in the week or so necessary to organize a control operation and locate and spray roosts. Locating the roosts can take days, since tracing flightlines can be done for only a brief period each day at dawn and dusk; it took 5 weeks, for example, to find and destroy the roosts at Jijiga in 1976. Nesting colonies, on the other hand, can be searched for throughout the day over wide areas from aircraft (Bruggers, Jaeger and Bourassa, 1983). Another disadvantage of a strategy of roost control is that damage can occur simultaneously in two or more widely separate areas when resources may exist for survey and control in only one area at a time. It is generally not practical to maintain more than one control unit with the specialized training and equipment and close supervision required for effective and responsible use of avicides.

Non-lethal alternatives. Traditional bird scaring is widely practised in the sorghum-growing areas in Ethiopia. This is commonly done from an elevated platform or termite mound within the field, from which a boy cracks a whip or slings dirt clods at the bird flocks. At best, this seems only to move birds from guarded to unguarded sorghum. There were, for instance, many bird scarers at Jijiga in 1976; four or more per hectare in places could not keep quelea out of their fields (M. M. Jaeger, personal observation).

Chemical or mechanical means to repel or frighten birds from fields are not widely used in Africa because the costs associated with their use usually are prohibitive, or they do not seem to reduce overall damage but rather move it to unprotected fields. One promising method has been to coat seeds with the chemical methiocarb (a carbamate insecticide marketed as Mesurol[R]) which, at low levels, consistently repels quelea and other ploceid pest species in laboratory tests (Shumake, Gaddis and Schafer, 1976; Shefte, Bruggers and Schafer, 1982). However, the results of field trials have been inconsistent, often due to insufficient or erratic bird pressure or high bird pressure on too small or too few test plots. Positive results have been reported under a variety of field circumstances (Bruggers, 1979; Erickson, Jaeger and Bruggers, 1980; Bruggers et al., 1981; Hamza et al., 1982). Ways are being sought to lower the costs involved by reducing the area within a field that is treated with methiocarb, either by spot treatments where birds are first seen to feed or by pairing a partial methiocarb treatment with more widespread visual cues (Bullard, Bruggers and Kilburn, 1983; Avery, 1985; Elmahdi, Bullard and Jackson, 1985). This approach may prove to be ineffective under circumstances where quelea are likely to continue sampling treated fields. This point will be expanded upon later when discussing the importance of feeding alternatives to the effectiveness of frightening devices. At present, methiocarb can be cost-effective in situations involving high-value crops, such as on seed-multiplication schemes, experimental plots or irrigated crops.

NORTH-CENTRAL UNITED STATES

Redwing damage to sunflowers

Sunflowers. maize and rice are the crops most damaged by redwings. These are grown principally in the central lowlands which are drained by the Mississippi. Missouri and Ohio Rivers (*Figure 3*). Sunflowers occur furthest to the north (*Figure 10*). concentrated in North Dakota and adjoining areas of northeastern South Dakota and northwestern Minnesota. Sunflower cultivation expanded between 1970 and 1980 from less than 100 000 ha to over 2 000 000 ha (Hothem, DeHaven and Fairaizl. 1988). During this period depredation by redwings also increased as ripening sunflowers occurred along a major corridor of redwing breeding and autumn flocking (Besser, 1978; refer to *Figure 3*). The task of resolving this problem was taken on by the Denver Wildlife Research Center (DWRC) which specializes in research on animal damage problems. In 1985 animal damage control (ADC) activities were transferred from the United States Department of the Interior. Fish and Wildlife Service, to the Animal. Plant and Health Inspection Service (APHIS) of the United States Department of Agriculture. Much of what follows is based on the work of DWRC scientists (*see* Guarino. 1984. for an overview). Redwing damage to maize (Stone *et al.*. 1972) and rice (Meanley. 1971) will be considered only where it interrelates with sunflower damage.

Patterns of bird damage to ripening sunflowers show general trends similar to those of quelea damage in Ethiopia: annual losses are a relatively small percentage of overall production. damage tends to be localized in the vicinity of roosts. and the location of major roosts is predictable. Losses in the three-state region (North Dakota. South Dakota. Minnesota) in 1979 and 1980 were estimated at 25 900 and 32 500 mT. respectively. representing 0.8 and 2.0% of the yields for those years (Hothem. DeHaven and Fairaizl. 1988). Only 2% of the 1488 fields sampled had damage greater than 10%. while 81% had less than 1% damage. Higher damage was associated with proximity to a marsh (Otis and Kilburn. 1988). Traditional autumn roosting areas where damage most regularly occurs are illustrated in *Figure 10*. It is in these four areas that much of the research on blackbird damage to sunflowers has been conducted.

Maize damage overlaps that of sunflowers in South Dakota and adjoining Minnesota where flocking redwings attack both crops. The spatial and temporal pattern of redwing damage in maize seems to be similar to that just described for sunflowers (Dyer. 1967; Stone and Mott. 1973; Wiens and Dyer. 1975; Somers *et al.*. 1981). Damage to both crops is concentrated around large August–September roosts at Sand Lake National Wildlife Refuge. South Dakota (*Figure 10*. area 4) (De Grazio. Besser and Guarino. 1969). The subsequent impact of these northern redwing flocks on ripening maize further south along the migratory route (*Figure 3*) probably diminishes since redwings seem to prefer maize. like sunflowers. in the earlier stages (milk and dough) of ripening (Besser. 1986). Meanley (1971) estimated that
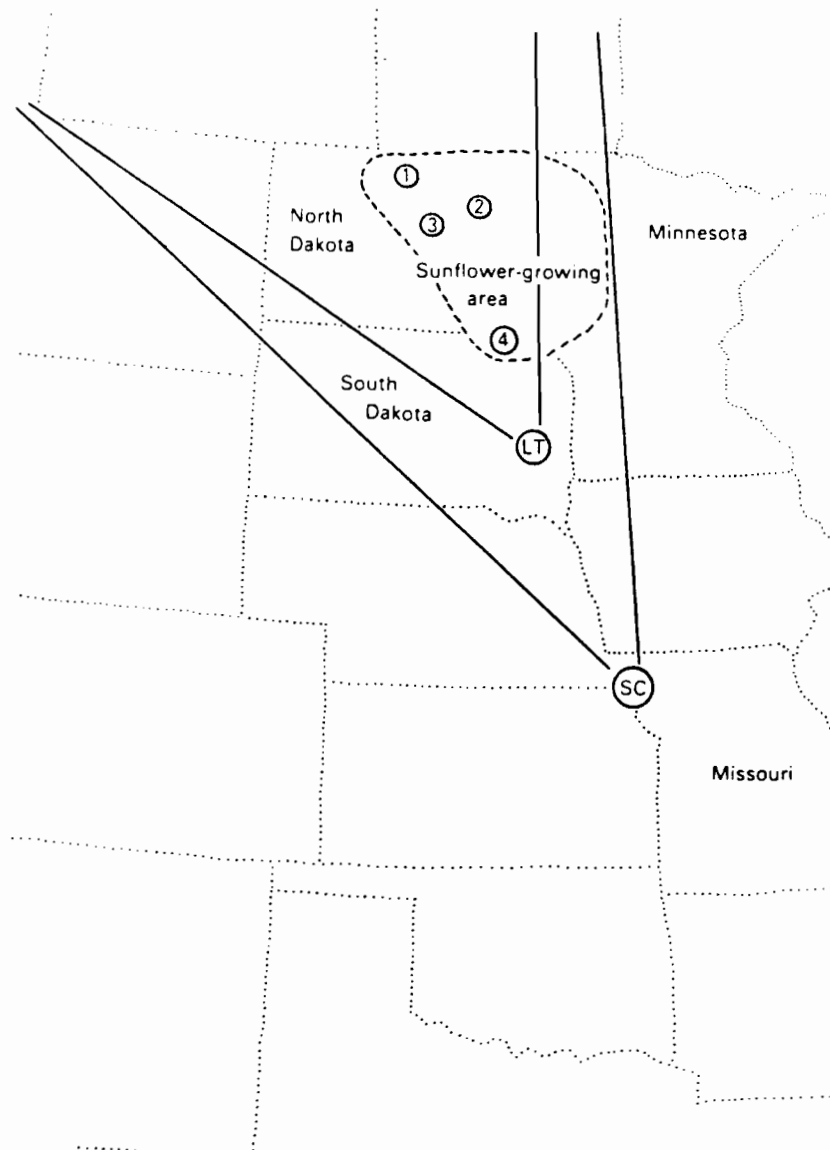
Figure 10. Nesting dispersal of male redwings marked at spring migratory roosts in relation to sunflower distribution (after Knittle *et al.*, 1987). LT = Lake Thomspon roost; SC = Squaw Creek National Wildlife Refuge roost; 1→4 = traditional autumn roosting areas.

only a very small percentage of these birds reach the rice-producing states in time to contribute to the damage done by locally breeding redwings.

Control of redwings in sunflowers

Research into the control of blackbirds in North America has taken a different direction from that for quelea in Africa. Emphasis has been on

finding ways to discourage the birds from feeding on crops. or to disperse the damage as opposed to local population reduction. Three general approaches have been pursued: frightening birds from fields. reducing the palatability of the crop. or reducing the attractiveness of its setting (*see* Besser. 1978. for a review).

Frightening and repelling methods.   Developing methods to frighten blackbirds from fields has been the main research thrust. It was hypothesized that this could be particularly effective if it was done by growers in the high-risk areas nearer the roosts. to disperse the damage by either dispersing the flocks or reducing the time they spent feeding in individual fields. Dispersing damage early might also reduce the losses by allowing for growth compensation (Guarino. 1984). Most of the damage by redwings occurs early (Cummings *et al.*. 1989). and sunflower heads can compensate for as much as 15% of seeds removed from a head during the soft-seed stage by increasing the size of remaining seeds (Sedgwick. Oldemeyer and Swenson. 1986). Compensation in maize. on the other hand. is often offset by secondary damage from insects or fungus (Woronecki. Stehn and Dolbeer. 1980).

The chemical frightening agent. 4-aminopyridine (4-AP). has been the most extensively tested means of scaring blackbirds from ripening sunflowers (Besser and Guarino. 1976: Besser. 1978: Guarino. 1984) and maize (De Grazio *et al.*. 1971. 1972: Stickley *et al.*. 1972. 1976: Dolbeer *et al.*. 1976: Knittle *et al.*. 1976). Ingestion of a bait coated with 3% 4-AP induces distress behaviour in fasted redwings after about 15 minutes (De Grazio *et al.*. 1971). followed by death 20–30 minutes later. This distress is characterized by loud and frantic vocalizations and erratic flight. termed 'towering' (Goodhue and Baumgartner. 1965: Schafer. 1981). Redwings in the area of an affected bird are attracted to it. and 'hover' over the spot in the field where the bird was first affected. They have then been seen to depart from fields: and it is maintained that flocks will depart from a large area given repeated exposure to affected birds (Besser. De Grazio and Guarino. 1973). However. flocks have also been seen to continue to feed in a field after the hovering response (Mott. Cummings and Naquin. 1982). In one study. for example. flocks remained in large sunflower fields in 19 of 30 situations where hovering was observed (Jaeger *et al.*. 1983a).

The effectiveness of 4-AP-treated baits (marketed as Avitrol[R]) remains questionable after years of research (Dolbeer *et al.*. 1976: Stickley *et al.*. 1976: Jaeger *et al.*. 1983a: Somers *et al.*. 1983; Kelley and Dolbeer. 1984). The treatment appears to have been effective in only some situations. The reasons for this ambiguity are unclear. and the issue has been very difficult to resolve. Proponents argue that the distress behaviour associated with 4-AP ingestion scares blackbird flocks from fields. but that in some cases too few birds become affected during a feeding foray to exert the additive effect necessary to move flocks out of the fields (Dolbeer *et al.*. 1976). This failure has been attributed to: (1) too low a ratio of treated to untreated baits (1 : 99): (2) loss or breakdown of the chemical treatment on the baits

(Guarino, 1984); (3) too large a bait particle size, resulting in birds breaking the bait and consuming an insufficient dose (J. Besser, personal communication); (4) absence of baiting lanes which provide access to baits (Besser, 1978); (5) removal of baits by insects (Woronecki and Dolbeer, 1980); or (6) too long a time from bait ingestion to distress, due to the presence of food in the bird's gizzard which slows the rate of 4-AP absorption (Sultana, 1985). The length of time to respond is especially important for those fields near the roost where many flocks feed for only a short time before departing, and where considerable damage may occur before the appearance of distressing birds.

Evaluation of the efficacy of 4-AP has been hindered by problems inherent in conducting field tests with flocking migratory birds. Flocking, flock mobility and roost turnover result in clustered damage and correspondingly high variance in damage estimates both within and among fields. When variance is high, the estimates of loss lack precision, and sample sizes necessary for statistical tests with reasonable power can be prohibitively large. In addition, when interpreting results it is often not possible to know when a treatment effect is due to avoidance or when it is the result of preference selection. This is an important distinction because if the result is due to preference selection, then in the absence of choices (i.e. few fields or all treated fields) the birds will likely feed in treated fields. As an example of preference selection, in 1983 fields of 'bird resistant' sunflower varieties were evaluated in North Dakota near traditional migratory roosts. Redwings clearly avoided these fields when more palatable sunflower seed was available in nearby fields; but once the alternative was gone they turned to these less-preferred varieties and completely destroyed them (M. M. Jaeger, personal observation). Another potential source of misleading results comes from tests where treated and control plots are close together so that flocks are more likely to select control fields in preference to the treated fields or other untreated fields, thereby inflating losses in the control fields.

Other commonly used means for frightening blackbirds from ripening sunflowers and maize are gas-powered exploders and firearms (Besser, 1978). For these to be effective where bird pressure is heavy requires considerable effort from the farmer. For instance, exploders must be moved regularly or the birds habituate. Similarly, keeping birds from fields by shooting at them may require several hours a day of patrolling for as long as the 6 weeks that sunflowers are vulnerable (Besser, 1978). These methods are probably more effective where feeding and roosting alternatives are available. However, the end result may not be to disperse the damage but rather to concentrate it in unprotected fields. Whatever their benefit, the use of these methods has not eliminated the problem, and alternative methods are still being sought.

Chemical repellents are not used on ripening sunflowers or maize because the seeds are protected by florets or husks which are difficult to penetrate with a spray. Methiocarb effectively repels redwings from treated foods in the absence of alternative foods (Schafer and Brunton, 1971) by a learned aversion (Rogers, 1974). The learned aversion (Reidinger and Mason, 1983)

is reversible as redwings continue to sample and detect the absence of the chemical (Rogers, 1978). Methiocarb seed-treatment is effective in protecting sprouting rice (Besser, 1973; Holler *et al.*, 1982) and sprouting maize (West, Brunton and Cunningham, 1969; Hermann and Kolbe, 1971; Stickley and Guarino, 1972; Ingram, Mitchell and Stickley, 1973) from birds. However, sunflower achenes impregnated with methiocarb were not effective as ground baits to repel blackbirds from ripening sunflowers (Jaeger *et al.*, 1983b). Redwings either preferred the soft seeds from the untreated sunflower heads to mature achenes on the ground, or had partially filled gizzards which impeded absorption of the methiocarb and reduced its effects (Thompson, Grant and Elias, 1981).

Food-choice context. It has been suggested that the presence of alternative feeding sites (i.e. untreated fields, harvested grain fields or uncultivated areas) may be an important determinant of whether or not control at the level of individual fields is likely to be effective (Dyer, 1967; Dyer and Ward, 1977; Weatherhead and Bider, 1979). This implies that where fewer alternatives exist, techniques such as frightening are less likely to be effective. Birds will, for example, habituate to the treatment. This assumes that flocks are able to identify alternatives, that they do not generalize a treatment broadly to crop type or stage of maturity, and that they can detect removal of a treatment by continuing to sample the area. Empirical evidence supports these assumptions; redwings are able to locate and exploit preferred crops, varieties (Fox and Linz, 1983; Dolbeer *et al.*, 1986; Mason *et al.*, 1986; Woronecki, Dolbeer and Otis, 1988) and stages of maturity (Somers *et al.*, 1981; Gartshore *et al.*, 1982; Avery and DeHaven, 1984; Cummings *et al.*, 1989). How do redwing flocks do this? We have previously explained how flocking may be an adaptation to finding and exploiting food that is spatially and temporally clumped. In the laboratory, redwings readily learn to distinguish food-choice situations (Beauchamp, Cyr and Houle, 1987) by continuing to sample the foods available to them (Rogers, 1978), or by observing the behaviour of conspecifics (Grant, 1978; Mason and Reidinger, 1981, 1983) and associating preferences or aversions with the attending visual cues (Mason and Reidinger, 1982).

Does treatment at the level of individual fields merely shift damage to untreated fields? The premise behind developing field treatments has been that they will disperse damage. There is no evidence that this happens regularly. Dispersing damage probably depends on the availability of alternative feeding sites and on the subsequent treatment of previously untreated fields to where flocks have shifted (Jaeger *et al.*, 1983a).

The choice context around traditional roosting sites can be manipulated. Besser (1978) and Wiens and Dyer (1975) point out that harvested fields can provide waste grain, weed seeds and insects upon which redwings feed (Mott *et al.*, 1972; Avery and DeHaven, 1984; Linz *et al.*, 1984) and should therefore not be plowed or tilled until after the sunflower harvest. In addition, decoy crops planted near the roosts can attract redwing flocks (Cummings *et al.*, 1987), and may be effective in dispersing damage when

used in combination with other methods. For example. in the high-risk areas nearer the roost, staggered planting of preferred sunflower varieties as lures could be used with the synchronous planting of less preferred varieties in the commercial fields where frightening is also used. Such an approach, however, necessitates considerable planning and co-ordination among farmers and land-use agencies. Dyer and Ward (1977) argue that changing agricultural practices to increase the diversity of food choices is the best solution in the majority of bird-pest problems (see Stone, 1980).

Population reduction. Destruction of major roosting concentrations of redwings with avicides could be a very cost-effective way to reduce damage to sunflowers (see Dolbeer, 1981, for an analysis of the cost-benefit of control with 4-AP). Reasons for not doing this have included: (1) adverse public opinion about killing birds; (2) lack of a practical and environmentally safe avicide formulated for spraying; (3) lack of information about the likely impact of redwing control on the populations of competing species; and (4) lack of sufficient information as to where and when the best opportunities for selective control exists. It is generally held that population reduction be considered only where the losses justify it and when other methods have proved to be ineffective or impractical. This seems to be the situation with regard to redwing damage to both sunflowers in the United States and ripening maize in southeastern Canada (Weatherhead and Bider, 1979; Weatherhead, Bider and Clark, 1980).

Finding an avicidal spray that is both environmentally safe and practical to use in a variety of field conditions has proved to be difficult. Organophosphates, such as fenthion, are considered unacceptable due to their potential hazard to non-target birds and other fauna associated with the areas in which redwings commonly roost. Birds of prey are especially vulnerable to fenthion used in bird control, through their feeding on dead and dying birds following spraying (Bruggers et al., 1989). The potential for this hazard, however, may be reduced with modifications in the spraying technique so as to kill target birds quickly and within the confines of the target area and then excluding predators from the site for several days following the spray. A small number of blackbird/starling roosts are sprayed in the United States each winter with the surfactant PA-14. This is a non-toxic detergent that interferes with feather insulation and, if applied during cold and rainy weather, results in death from exposure (LeFebvre and Seubert, 1970; Weatherhead, Bider and Clark, 1980; Schafer, 1981). The weather conditions necessary for this to be effective limit its usefulness. Chloro-para-toluidine (CPT) is a promising avicide that is being tested currently as a roost spray (Linz, Mott and Schafer, 1988). It acts by interfering with kidney function and is potentially safe for most vertebrate predators and scavengers (Schafer, 1984). A major obstacle to the use of pesticides against redwings is that most roosts are over water where the application of toxic chemicals is prohibited or severely restricted.

Widespread population reduction might be compensated for by an increase in the populations of competing species (Dyer and Ward, 1977; Weatherhead

et al., 1980). Compensation might be most dramatic where a competitive imbalance is already occurring. For example, Besser *et al.* (1984) and Besser (1985) suggest that in North Dakota yellowheads are increasing in number and redwings decreasing, presumably due to competition for wetlands nesting sites. There are no unequivocal examples of a compensatory increase in the abundance of another species due to quelea control in Africa. A possible example may be the displacement of quelea by the golden sparrow (*Passer luteus*) along the southward-moving edge of the Sahara. While this seems in large part due to habitat changes associated with desertification, the process may be accelerated by intensive quelea control (for example. Senegal River Valley; G. Morel, personal communication). Limiting control to selected targets probably reduces the potential for disruption among competing species. For instance, there was no evidence for a reduction in the numbers of quelea nesting colonies following 3 years of control in the Awash River Valley.

Developing strategies for selective population reduction of migrating redwings requires information on the seasonal movements of those birds likely to cause damage and the timing and location of their largest concentrations. Ringing with numbered leg bands has been the principal means of obtaining such information (Burtt and Giltz, 1977; Dolbeer, 1978, 1982). Although thousands of ringed redwings have been recovered over many years, the information obtained is still insufficient on which to develop a control strategy. Because of the relatively few recoveries and the often long interval between ringing and recovery, it is difficult to make meaningful inferences about short-term group movements. Ringing was improved upon by the addition of colour-coded leg streamers which allow for sight recoveries (Guarino, 1968). However, a breakthrough came with the development of a technique for mass-marking birds in roosting or nesting aggregations by spraying fluorescent particles (suspended in a liquid adhesive) from aircraft (Jaeger *et al.*, 1986). This method is now being used to study redwing movements (Otis, Knittle and Linz, 1986; Knittle *et al.*, 1987). Mass marking can be used alone or in combination with morphological or physiological markers to determine the direct, short-term movements of large groups of birds (James *et al.*, 1984; Jaeger *et al.*, 1986; Linz, 1986).

Population reduction in relation to the seasonal distribution of redwings

Late summer–autumn roosts.   Destruction of those roosting aggregations of redwings actually engaged in damaging sunflowers is clearly the most selective strategy of population reduction to reduce losses. The potential number of roosts that would have to be treated, however, suggests that this may not be the most practical or environmentally sound strategy. Compared to the spring migration, the autumn migration will have: (1) peak numbers of blackbirds, since this follows the breeding season: (2) smaller and more scattered roosts; and (3) a longer duration of migration. Four roosts, for

example, were found in an 800 km² study area in North Dakota in the autumn of 1986 (within the traditional sunflower damage area number 2, *Figure 10*). From late August to early October, an estimated 250 700 redwings and 71 200 yellow-headed blackbirds migrating through the area used these roosts and destroyed an estimated 306 mT of sunflowers (Linz, Knittle and Cummings, 1988). The pattern of roost turnover from late August to late September tended to be bimodal, suggesting the need for at least two treatments per roost to achieve effective crop protection. In addition, numerous small and scattered roosts are common at this time (e.g. area number 3, *Figure 10*: Besser, Berg and Knittle, 1979; Jaeger *et al.*, 1983a), making roost control by a single control team time-consuming and environmental contamination more widespread. A more selective strategy of controlling only the principal autumn roost sites may be beneficial, particularly when and where damage tends to be highest.

Winter roosts. Large winter roosts in the southern United States are potentially important targets for selective control if the redwings that damage crops in a particular area, such as the eastern Dakotas, tend to overwinter together. Ringing was used to determine the winter location of redwings that damage maize (and sunflowers) in the vicinity of Sand Lake National Wildlife Refuge, South Dakota (*Figure 3*; traditional roosting area number 4, *Figure 10*). Between 1961 and 1974, 23 562 redwings were ringed at Sand Lake, 80% were captured during the damage period (Besser, De Grazio and Guarino, 1983). Annual numbers of blackbirds roosting at Sand Lake during the damage period ranged from an estimated 0.7 million to 1.8 million, and these were mostly redwings (Besser, De Grazio and Guarino, 1973). Eighteen male redwings ringed during the damage period were eventually recovered in winter roosts, 11 from the coastal plain of eastern Texas. The remaining winter recoveries extended 1617 km north to south along the migratory corridor illustrated in *Figure 3*, suggesting that the winter range can be extensive (De Grazio, Besser and Guarino, 1969). These findings are consistent with the analysis of ringing recoveries of Dolbeer (1978, refer to his Figure 4c, p. 26). Other studies have shown that winter roosts can be made up of redwings from a wide nesting area (Stewart, 1977; Dolbeer, 1978, refer to his Figure 6c, p. 29). For example, eight sightings from 2618 male redwings ringed with colour-coded leg streamers at a winter roost in the northern panhandle of Texas in 1979 extended from western Colorado to eastern Kansas, or 1100 km west to east (Royall and Cummings, 1981). Dolbeer (1978, 1982) concluded from his analysis of ring recoveries that local breeding populations are dispersed in winter, and ·reduction of populations of redwings that cause localized late-summer agricultural damage probably cannot be practically achieved through the mass killing of blackbirds in a few winter roosts in the southern United States.·

Spring migratory roosts. Attention is now turning to the large spring migratory roosts that form in February and March along the main corridor of migration (*Figure 3*) that passes north through the Dakotas (Otis, Knittle

and Linz, 1986; Knittle *et al.*, 1987). Here the number of major roosts seems
to be few. In terms of a strategy for selective control, it is of particular
interest to know if a traditional roost exists that contains a high percentage
of the redwings that migrate back and forth through the sunflower-growing
area. The largest spring migratory roost along this route appears to be the
one in northwestern Missouri at the Squaw Creek National Wildlife Refuge
(*Figures 3* and *10*). In March 1982, an estimated 7.5 million male redwings
were marked in this and a nearby roost with aerially applied fluorescent
particles (Knittle *et al.*, 1987). Of the 5526 male redwings collected on
breeding territories to the north of Squaw Creek in May and June, 10.2%
or 565 had the marks, while none of the 741 birds collected to the south
were marked. Although marked redwings were found over a broad front
east to west, the main route of dispersal appears to have been to the
northwest, encompassing the sunflower area (*Figure 10*). From these
recoveries it is not possible to know what percentage of the adult male
redwings that migrate through the sunflower area in the autumn pass through
Squaw Creek. The highest percentage of marked recoveries was 28% from
just north of the sunflower area in southern Manitoba, Canada. However,
the actual percentage of male redwings passing through the sunflower area
that had also come through Squaw Creek was probably much higher. An
estimated 56% of the male redwings at Squaw Creek had been marked,
and indications were that the marker had worn off a high percentage of
birds before collections were made. There were also large geographic gaps
in the collections from where higher percentages of marked recoveries were
possible. Furthermore, the very large numbers of male redwings estimated
to roost at Squaw Creek (Knittle *et al.*, 1987) compared with the 1–2 million
males estimated to breed annually in North Dakota (Besser *et al.*, 1984,
1987) suggests that a high percentage of the North Dakota male redwings
pass through Squaw Creek.

Another major spring migratory roost regularly occurs at Lake Thompson,
South Dakota, just to the south of the sunflower-growing area (*Figure 10*).
Due to its closer proximity, it was anticipated that this roost would have a
relatively greater impact on sunflower damage than the one from Squaw
Creek. To investigate this, the Lake Thompson roost was sprayed with
marker in March 1983 and an estimated 2.4 million (80%) male redwings
were marked (Knittle *et al.*, 1987). The pattern of marked recoveries
supported the potential importance of this roost as a target for selective
control (*Figure 10*). Much additional information, however, is needed about
these spring roosts (turnover rates, routes of onward migration, numbers of
birds, sex and age composition) before being able to model the likely impact
of selective roost destruction on later sunflower damage.

Summary of the implications of flocking behaviour to management of quelea and redwings

1. Quelea and redwings migrate along the same routes each year, tending
    to use traditional roosting, nesting or feeding areas. The timing and

path of movement depends on the seasonal availability of food so that communal aggregations are often found in association with ripening crops. As a consequence, the damage is typically concentrated around predictable roosting sites where losses can accumulate rapidly.

2. Chemical or mechanical techniques have been sought which disperse damage away from fields near roosts. In general, these methods have given inconsistent results in the treated fields and have not been demonstrated to disperse damage. Flocks seem more likely to abandon treated fields where acceptable alternative feeding sites occur, and alternative sites usually include untreated crops to where damage can be shifted. The available feeding choices, therefore, seem to be an important determinant of whether or not control methods involving preference choices (e.g. the use of less-preferred varieties) are likely to be effective. Manipulating feeding choices may be impractical in many situations.

3. Destroying roosting or nesting aggregations can be a relatively cost-effective way to reduce losses when directed at those aggregations either causing or likely to cause damage. The most selective strategy for population reduction will be situation specific, involving annual control at a predictable time and place, depending on the local pattern of migration and flocking. The major disadvantage of this approach is the potential for environmental and non-target contamination by pesticides.

Acknowledgments

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